

## POLLINATION ECOLOGY IN MONTANE COLORADO:

### A COMMUNITY ANALYSIS

Andrew R. Moldenke<sup>1</sup>  
&  
Patricia G. Lincoln<sup>2</sup>

#### ABSTRACT:

Synecological pollination studies of communities in montane Colorado revealed very low species richness of all types of pollinators although flowers were abundant. In every community less than 8% of the non wind-pollinated plant species attract more than 60% of the resident vector species. A large majority of the pollinator species and nearly all the pollinator individuals in each of the five communities are generalist feeders; bumblebees are preeminent in all environments and muscoid flies are prominent in the alpine tundra and forests. In all communities selfing as the habitual mode of reproduction is very frequent (20% of the total flora), and increases to 48% of the flora in the alpine tundra. Pollinators are most abundant in the physiognomically open fescue grassland, sage and alpine tundra communities, but are most diverse in the lower altitude grassland and sage. Pollinators are least abundant and diverse in the aspen and spruce-fir forest communities. Specialist pollinators comprise 8% to 22% of the total resident pollinators; specialist species are two to five times richer in the open communities than in the forests. Pollination characteristics of the five communities parallel results obtained in subalpine and alpine California.

#### INTRODUCTION

Pollination systems comprise the direct or indirect interactions of two trophic levels, forming a dynamic, yet somewhat cohesive, ecological subunit of a community. This plant/herbivore interface can be readily studied in terms of species diversity and distribution, resource utilization and niche packing. Analysis of pollination syndromes in different community types provides a means to compare the operation of these systems under a variety of environmental regimes. Community-wide studies also place the examination of specific plant/pollinator relationships in a broad ecological context. The necessity of viewing the coadaptations of pollinators and their plant hosts as components of the systems in which they operate and not simply as the results of reciprocal

<sup>1</sup>lc/o Biology Dept., Univ. of Santa Clara, Santa Clara, Ca.

<sup>2</sup>Division of Natural Sciences, Univ. California, Santa Cruz, Ca.

effects on a one-to-one basis has been pointed out by many authors (Heinrich and Raven, 1972; Macior, 1971; Baker, 1963).

Previous analyses of pollination systems by our group have indicated that over-all physical environment has a preeminent role in determining which adaptive strategies are viable and, in turn, the manner in which these systems must function (Moldenke, 1975, 1977, 1979; Cody et al., 1977; Simpson et al., 1977). However, for any one particular species, the success of any foraging strategy by pollinators or any means of outbreeding by plants is highly dependent upon the spatial arrangement and competitive interactions within the community in which they operate. Therefore, predictions about the specific composition and functioning of these strategies in individual community types cannot be made with precision for each species.

Our investigations were conducted near the Rocky Mountain Biological Laboratory in Gothic, Colorado, with study sites ranging from 3,800 m to 4,300 m in altitude. According to our basic null hypothesis that the over-all climate determines the possible outcomes of niche structuring to a very great extent, the pollination systems in the component community types should be very similar to those previously delineated in communities in the Sierra Nevada of California (Moldenke, 1975, 1977), despite the differences in the floristic and faunistic elements of the two areas. The present study was designed to test predictions generated from results in California and a general knowledge of the major groups of pollinators. Our predictions based on theory presented in Moldenke (1975) about the over-all diversity and adaptive strategies to be found under the general environmental regime in Colorado are as follows:

1. Total pollinator diversity and biomass should be low relative to previously documented communities at much lower altitudes; both measures should increase in Colorado at lower altitudes and in physiognomically more open habitats where the microclimate would favor insect activity.

2. There should be many more generalist pollinators than specialists, unlike the regions of warm Mediterranean climate on the West Coast of the United States. The ratio of generalists to specialists should be particularly high in physiognomically closed forest habitats where shade places a premium on poikilotherm energy conservation and should preclude the option of treating resource presentation in a "coarse-grained" (Levins, 1968) fashion. This ratio should increase with altitude as the severe unpredictable climate would favor a resource utilization strategy that takes advantage of whatever is available to an even greater extent.

3. Many plants should be autogamous and not visited by pollinators; their number should increase at higher altitudes.

4. A few species of plants should be heavily visited by many different pollinators in all vegetation types and altitudes, since the pollinators will concentrate upon whichever species offer the best reward as the season progresses, regardless of the relative total pollinator abundance.

#### METHODS

Research was conducted at five sites within a 100 mile radius of the Rocky Mountain Biological Laboratory in Gothic, Colorado. We selected one to two study sites in each of the following community types recognized by Langenheim (1962). In none of the areas studied was the introduced honeybee, Apis mellifera, a resident species. A 0.5 km<sup>2</sup> plot was studied intensively in each community type. Research sites were visited on a rotating basis whenever weather permitted from the third week in June through the last week in August, 1974.

a) Alpine Tundra: Cumberland Pass, Gunnison County, 4,000-4,100 m; and Mesa Seco near Slumgullion Pass, Hinesdale County, 3,900-4,100 m. Communities of caespitose perennials dominated by Festuca brachyphylla, Poa alpina, Carex engelmannii, Trifolium dasyphyllum, Potentilla diversifolia, Erigeron leiomerus, Achillea lanulosa, Phlox caespitosa and Oreoxis alpina.

b) Mature Aspen Forest: Rocky Mountain Biological Laboratory, Gunnison County, 3,200-3,500 m; and Spring Creek Road, near Almont, Gunnison County, 3,000-3,300 m. Closed canopy Populus forest with understory dominated by Thalictrum fendleri, Ligusticum porteri, Agropyron trachycaulon, Bromus richardsonii, Lathyrus leucanthus, Festuca thurberi, Aster occidentalis, Pedicularis grayi, Calochortus gunnisoni and Senecio serra.

c) Sagebrush: Jack's Cabin Cutoff Road, 15 miles southeast of Crested Butte, Gunnison County, 3,130-3,230 m. Open range with Artemisia tridentata, Lupinus floribundus, Castilleja linearifolia, Chrysothamnus viscidiflorus, Achillea lanulosa, Arenaria congesta, Muhlenbergia montana, Erigeron racemosus, Stipa lettermannii and Wyethia arizonica dominant.

d) Fescue Grassland: Gothic, Gunnison County, 3,125-3,275 m; and Washington Gulch, near Crested Butte, Gunnison County, 3,150-3,300 m. Dominant plants are Festuca thurberi, Potentilla gracilis, Achillea lanulosa, Taraxacum officinale, Erigeron speciosus, Muhlenbergia filiformis, Helianthella



quinquenervis, Bromus polyanthus and Linum perenne.

e) Spruce-fir Forest: Lake Irwin, Gunnison County, 3,380-3,485 m; and Washington Gulch, Gunnison County, 2,900-3,200 m. Picea pungens forest with P. engelmannii and Abies lasiocarpa and understory of Lupinus argenteus, Vaccinium myrtillus, Bromus richardsonii, Agropyron trachycaulon, Agrostis scabra, Carex geyeri, Pedicularis racemosa, Achillea lanulosa, Polemonium delicatum, Mertensia ciliata, Arnica cordifolia and Haplopappus parryi.

Censusing techniques employed for both plant and pollinator abundance are described in Moldenke (1975). Relative abundance of plant species was determined by censusing ten replicate 10 x 10 m random plots in each community; an additional list of all species present but not encountered in the census was also kept. Measurements on floral size and number of flowers per plant were made with the aid of the reference herbarium at the laboratory and a series of at least five randomly selected field individuals. All insects encountered visiting flowers during the course of the research were collected and their floral host recorded. Collection technique never entailed remaining at one particular plant or subarea, but rather took the form of a continuously moving search throughout the region under study. Paths were not chosen under a statistical format that completely assures that all portions of the study areas were visited with equal frequency; hence, if plant species are not randomly distributed, the results may not be unbiased. Plant self-compatibility studies carried out by Constance Rutherford (pers. comm.) entailing bagging with 0.4 mm mesh and known compatibility data from former studies (Moldenke, 1971) were used to supplement field observations on the percentage of successful seed set. Determinations of compatibility could be made for approximately 60% of the flora.

Not every insect which visits a flower is an effective pollinator nor is the relative abundance of all species of floral herbivores an index of their relative contribution to outcrossing. In the absence of autecological studies with marked pollen grains on each species of insect observed to utilize flowers as a food resource, our own subjective judgment based on field observation of intrafloral behavior, insect morphology and fidelity to a particular plant species by individuals for short extents of time are the basis of our judgment as to whether any significant pollination may be attributable to a particular species. In this paper no judgments are made as to the relative efficiency of different species of vectors servicing the same species; all species that on the above grounds are deemed potentially significant vectors are so treated in Table 2, for instance. Infrequent but consistent visitation by a bumblebee to a



flower in which it usually contacts the reproductive structures weighs equivalently with an abundant syrphid species which feeds heavily upon one particular plant species, but seldom contacts the stigma. Since insect vectors are generally infrequent in the areas under study, if any bias exists it emphasizes the role of infrequent vector species at the expense of the "habitual selfer" category.

Collected insect specimens were identified whenever possible by taxonomic experts. Special thanks are due to David Inouye, Robbin Thorp, Roy Snelling, Uri Lanham and P. Timberlake for their determinations. Additional determinations were made in the reference collection at the University of Colorado. Plant species were identified with reference to the herbarium of the Rocky Mountain Biological Laboratory, Barrell (1969) and Weber (1972).

## RESULTS

### I. POLLINATOR DIVERSITY AND FREQUENCY OF POLLINATION MODE

#### A. Total Floral-herbivore Diversity

Flower visitor diversity is highest within the unshaded sage and fescue grassland communities (mean species count=152; Table 1). Total species count of flower herbivores decreases by 29% in alpine communities and by 46%-51% in the aspen and spruce-fir forest communities compared to the levels supported in unshaded sites. The total number of individual floral-herbivores of all types was highest in the grassland communities, total floral-herbivore individuals decreasing by 45% in the alpine and by 71%-78% in the forest communities (Table 1). The count of individual insect flower feeders may be a misleading assay of trophic energetic relations, since different species may differ widely in their body size and energetic requirements. Relative biomass measurements were approximated by the product of linear dimensions of the bodies (appendages excluded)(Moldenke, 1975). Insect biomass, indeed, followed a similar pattern; biomass of floral-herbivores in fescue grassland was approximately three times that in the alpine and forest communities.

The most important floral-herbivore as well as pollinator group in all of the communities studied is the Apoidea (bees), in terms of diversity, number of individuals feeding upon flowers, and the percentage of the flora relying upon them for pollen transfer. Direct comparison of bee diversity patterns may be a better indicator of long-term species packing phenomena than comparisons between other groups of flower-visitors, since we know much more about the behavior and distribution of bee species than other insect floral-herbivore groups and since the entire life cycle of all bee

TABLE 1.

	ALPINE		ASPEN		SAGE		FESCUE		SPRUCE-FIR	
	Total Spec.	Total Indiv.	Total Spec.	Total Indiv.	Total Spec.	Total Indiv.	Total Spec.	Total Indiv.	Total Spec.	Total Indiv.
Solitary Bees	21	130	17	29	50	150	51	240	13	30
Halictine Bees	5	7	5	14	5	17	8	96	5	23
Bumblebees	5	110	7	36	10	105	11	306	7	97
Hover Flies	28	81	10	26	9	21	30	120	14	44
Beeflies	3	5	0	0	11	38	6	13	3	4
Beetles	3	3	5	22	7	41	10	23	9	27
Hummingbirds & Sphinx Moths	2	3	1	14	1	11	2	28	1	4
Butterflies & Moths	21	55	4	7	17	29	11	26	8	12
Wasps	1	1	4	4	15	31	6	6	6	7
Sawflies	5	7	3	10	3	4	4	14	1	1
Primitive Flies	2	11	4	8	3	4	4	8	3	10
Muscoid Flies	10	118	8	37	9	16	12	68	5	19
Other Groups	3	6	2	5	5	14	5	12	2	2
Total	109	537	70	212	145	481	160	960	77	280

TABLE 1. Flower-herbivore Diversity and Abundance

Hummingbirds are not distinguished to species; their abundance is the estimated total number of territorial birds working the region and relative floral resource use, rather than total number of floral visitations observed.

TABLE 2.

POLLINATION MODE	ALPINE	ASPEN	SAGE	FESCUE GRASSLAND	SPRUCE- FIR
WIND	16 (17%)	16 (21%)	9 (12%)	20 (17%)	14 (19%)
SELF	43 (48%)	19 (25%)	19 (24%)	35 (21%)	19 (25%)
Obligate Self & Apomictic	10 (11%)	10 (13%)	8 (11%)	6 ( 5%)	7 ( 9%)
BUMBLEBEE	29 (31%)	19 (25%)	22 (31%)	41 (35%)	18 (24%)
SOLITARY BEE	15 (16%)	12 (16%)	19 (27%)	31 (26%)	9 (12%)
Specialist Solitary Bee	10 (11%)	5 ( 6%)	13 (19%)	16 (13%)	3 ( 4%)
HALICTID BEE	4 ( 4%)	6 ( 8%)	1 ( 1%)	25 (21%)	4 ( 5%)
SYRPHID	19 (21%)	6 ( 8%)	1 ( 1%)	21 (18%)	11 (15%)
MUSCOID	9 (10%)	8 (10%)	0 ( 0%)	8 ( 7%)	4 ( 5%)
BUTTERFLY	11 (12%)	1 ( 1%)	5 ( 7%)	6 ( 5%)	5 ( 6%)
HUMMINGBIRD & SPHINX MOTH	3 ( 3%)	5 ( 6%)	4 ( 5%)	8 ( 7%)	3 ( 4%)
BEEFLY	0 ( 0%)	0 ( 0%)	6 ( 8%)	3 ( 3%)	2 ( 2%)
WASP	0 ( 0%)	1 ( 1%)	4 ( 5%)	1 ( 1%)	3 ( 4%)
OTHER GROUPS		beetle-1 sawfly-1	beetle-1	beetle-3 sawfly-1	beetle-1



species is obligately dependent upon flowers; whereas that of most other flower eating groups is not. The pattern of reduced species richness in alpine and subalpine regions, relative to lower altitudes is evident when examining only bees as well.

In Colorado, both Forest and alpine communities support roughly equivalent numbers of bee species, approximately one-half the number in the open sage and grassland communities (28:67; Table 1). Our results indicate that syrphid and muscoid flies are the exclusive pollinators of ten percent of the alpine flora in Colorado. A larger sample size and investigations during subsequent years are certain to reduce the number of plants serviced exclusively by these fly groups, but we are confident that it will not significantly alter the percentage crosspollinated most frequently by these groups.

Wind pollination is the rule for the dominant plants in all communities (e.g., Abies, Agropyron, Artemisia, Bromus, Carex, Festuca, Muhlenbergia, Picea, Poa, Populus, Thalictrum). On a species-by-species basis wind pollination is least frequent in the physiognomically open tundra, fescue and sage communities (Table 2). In the latter two communities the decrease in relative frequency of wind-pollinated species correlates with a significant increase in the presence of potential pollinator insect taxa. In the tundra community of California, studies have shown (Moldenke, 1975) that most of the "wind-pollinated species" reproduce in fact by selfing or apomixis; we did not undertake parallel breeding studies in Colorado tundra.

#### B. Community Pollination Modes and Relative Pollinator Group Frequency

The alpine tundra communities are characterized by relatively low diversities of solitary bees, bumblebees and muscoid flies and high diversities of syrphid flies and

TABLE 2. Pollination Syndromes of the Alpine and Subalpine Colorado Flora

The number represents the total number of resident species utilizing a particular mode; the figure in parentheses is the percentage of the total species in the community utilizing a particular mode. Percentages total to more than 100% because some plant species are characterized by more than one mode. Obligate selfing and specialist bee are subsets of the more inclusive categories. Many species which probably habitually self nearly all their seeds in most areas are also included under the category of their infrequent vectors, under the assumption that such outcrossed seed that is produced may occasionally possess competitive advantages.

butterflies. All other groups essentially are absent (Table 1). The percentage of the total pollinator individuals which are solitary bees is high (24%), due to the extreme abundance of a single species, Panurginus bakeri, a Potentilla specialist. Although there are only two common bumblebees in the alpine tundra communities studied, they comprise more than one-fifth of the total pollinator biomass. The individuals of these species are relatively large and colony sizes are apparently small. Queens are encountered as frequently as workers on the flowers and may be encountered throughout the growing season. Anthomyiid flies account for one-quarter of the biomass of pollinators in these communities; none are suspected of specialized feeding habits. While syrphid flies and butterflies are diverse in total number of species, together they comprise only a quarter of the biomass.

From the standpoint of effectiveness as pollinators, high percentages of the alpine flora use bumblebee, syrphid fly, muscoid fly and butterfly pollination modes; beefly pollination is absent (Table 2). The occurrence of high winds and localized clouds over the high peaks in the afternoon restricts most pollinator activity in alpine tundra environments to the late morning hours after the ground temperature has risen, but before shading by the clouds. Even during these favorable periods, pollinator flight activity is generally limited to very short flights. Bumblebees are at a special advantage in these conditions, since their very low surface to volume ratio, pronounced insulatory properties and physiological capability to thermoregulate permit them to exploit floral resources during periods when other pollinators are inactive because of thermal stress. The alpine flora benefits directly from this increased level of activity, for even during extremely cool and windy periods, bumblebees frequently walk between the flowers of caespitose species. The cost of thermoregulatory floral visitation under cool ambient temperatures and the added cost of brooding within the nest requires more floral visitation for nectar than required by solitary non-thermoregulatory bees of equivalent body proportions (Heinrich, 1975), thereby further enhancing the crosspollination of the resident flora.

Both forest communities are characterized by very low levels of flower feeding individuals and total species diversity (Table 1). Pollination in the spruce-fir forests is largely restricted to that carried out by bumblebees and syrphid flies; jointly they visit 39% of the insect pollinated species (Table 2). Solitary bees, halictids, beeflies and wasps are infrequent and collectively pollinate less than 15% of the flora. Most pollinator activity is confined to small forest glades where understory bloom is profuse and sunlight is not intercepted by the forest canopy.

The understory in the aspen forest is much more dense, usually 100% cover. Most of the plants in the somewhat disturbed regions of the aspen understory that we studied flower profusely, even in the shade of the canopy, which is not as dense as that of even an immature spruce-fir forest. Hummingbirds are frequent, though not as abundant as in the glades or the meadows. Muscoid flies, solitary bees, bumblebees, syrphids and beetles are all abundant flower visitors, but none of the groups are species rich. Beeflies and wasps are absent from the aspen forest, except for the specialist-feeding pollen-collecting masarid wasp, Pseudomasaris marginalis, which occasionally strays into the forest edge in search of Phacelia. Unlike all other communities which have their own characteristic pollinator fauna, the aspen forest shares the fauna, as well as a large percentage of the flora, of other communities. Only 5% of the pollinator species encountered in the aspen forest were not found in greater abundance in other community types. Most of the pollinators collected in the aspen forest were found near to the forest edge; whether this represents the existence of a permanent ecotonal element within the pollinator fauna or simply the presence of higher levels of insolation, and consequently insect abundance, is not known. The solitary bees (Osmia spp.), the muscoid fly Lasiops septentrionalis and the syrphid Cartosyrphus tarda are the most abundant aspen forest pollinators; they frequent legumes, composites and umbellifers, respectively.

Sagebrush communities at subalpine elevations have the high pollinator abundances and diversities characteristic of fescue grassland, but are noticeably depauperate in comparison to sage at only 2,000 m in the vicinity of Gunnison, Colorado. Bumblebees are abundant and diverse in the sage community; they account for the pollination of 48% of the insect pollinated flora. Solitary bees are more diverse in the sage than in any other community type; they comprise more than one-third of the total flower-feeding species (Table 1) and visit 42% of the insect pollinated flora (Table 2). The most diverse group of solitary bees are the Osmia species, which frequent Penstemon, Lupinus and composites. Specialist solitary bees visit nearly 20% of the total plant species present. Beefly and wasp pollination are both important elements within the sage community. Muscoid and syrphid flies are conspicuous by their absence.

The fescue grassland communities are characterized by the highest diversity and abundance of insect pollinators, as well as the greatest frequency of hummingbirds (Table 1). Grassland supports the highest diversities of all individual flower feeding groups, except butterflies, wasps and bee-flies. As in the sage community, more than 40% of the total pollinator species are bees. Solitary, halictid and bumblebees are all very diverse relative to neighboring



communities. Halictid bees are significant pollinators of more than 25% of the total resident flora (Table 2) and comprise 10% of the total pollinator abundance. The most abundant solitary bees are members of the genera Osmia and Panurginus. Beeflies are present, but not abundant. Muscoid and syrphid flies are abundant (about 20% of the total pollinator individuals) and figure significantly in the pollination of 20% of the insect pollinated flora (Tables 1 & 2). They are conspicuously more abundant in more mesic grasslands, where they heavily visit umbellifers and, to a lesser degree, composites. As in California marsh/meadow communities, muscoid flies reach their highest diversity in the "hydric" (Langenheim, 1962) communities; in this particular region of Colorado this plant association was too limited in width wherever it occurred to permit direct comparison to the plant communities of wider geographic extent. There are no tachinid muscoid pollinators at these elevations, again paralleling subalpine studies in California.

## II. RESOURCE UTILIZATION STRATEGIES

### A. Generalist vs. Specialist Feeders

Table 3 lists the most abundant pollinator species which have specialized feeding habits in the areas studied. We define "specialist feeder" as those species of pollinators which confine their feeding to only one species, to a series of congeneric species of plants or occasionally to morphologically similar non-congeneric Compositae and Leguminosae. We have designated species as specialists or generalists on the basis of feeding habits observed under localized conditions; thus, while generalist feeders at these sites are probably catholic in their preferences throughout their range, "specialists" may or may not be restricted to the same plant resource in adjacent regions. Rare species have been excluded from this analysis since the distinction between a rare generalist and a specialist is moot.

The percentage of the total pollinator species which are specialist feeders ranges from 8%-13% in the forest communities to 17%-21% in the alpine tundra and fescue grassland communities and to a high of 22% in the sage. Diversity measures (i.e., H'; Margalef, 1957), in which both total species count and relative abundance are considered,

TABLE 3. Specialist Pollinators

Specialist is defined solely in terms of the manifest behavior of each insect taxon at each particular research site. These plant listings should not be interpreted necessarily as genetically determined host preferences, although some may well be.

TABLE 3.

POLLINATOR SPECIES	PLANT(S) VISITED	COMMUNITY TYPE(S) IN WHICH COLLECTED				
		ALPINE	SPRUCE	ASPEN	PESCUE	SAGE
<u>BEES</u>						
<u>Andrena birtwellae</u>	<u>Potentilla</u>	X			X	X
<u>A. cyanophila</u>	<u>Potentilla</u>				X	
<u>A. n. sp.</u>	<u>Erigeron, Aster</u>			X	X	
<u>A. n. sp.</u>	<u>Erythronium</u>		X		X	
<u>A. n. sp.</u>	<u>Salix</u>	X				
<u>Anthidium maculosum</u>	<u>Phacelia</u>				X	
<u>A. emarginata</u>	<u>Phacelia</u>				X	
<u>A. emarginata</u>	<u>Trifolium</u>	X				
<u>A. tenuiflorae</u>	<u>Trifolium</u>	X				X
<u>A. sp.</u>	<u>Trifolium</u>	X				
<u>Anthocopa abjecta</u>	<u>Penstemon</u>					X
<u>Anthophora sp.</u>	<u>Compositae</u>					X
<u>Ashmeadiella sp.</u>	<u>Compositae</u>					X
<u>Colletes consors</u>	<u>Mertensia</u>	X	X			X
<u>C. nigrifrons</u>	<u>Potentilla</u>	X		X	X	X
<u>C. phaceliae</u>	<u>Compositae</u>					X
<u>C. woottonae</u>	<u>Lupinus</u>					X
<u>Dufourea fimbriata</u>	<u>Potentilla</u>			X		X
<u>D. maura</u>	<u>Campanula</u>			X	X	
<u>Formicapis clypeata</u>	<u>Potentilla</u>				X	
<u>Heterosarus bakeri</u>	<u>Compositae</u>				X	
<u>Mezachile melanophaea</u>	<u>Lupinus, Trifolium</u>	X		X	X	X
<u>Mezachile sp.</u>	<u>Chaenactis</u>					X
<u>M. sp.</u>	<u>Compositae</u>				X	X
<u>M. sp.</u>	<u>Compositae</u>				X	X
<u>M. sp.</u>	<u>Compositae</u>				X	
<u>Melissodes hymenoxidis</u>	<u>Chrysothamnus</u>					X
<u>M. sp.</u>	<u>Compositae</u>					X
<u>Osmia bucephala</u>	<u>Lathyrus</u>			X		X
<u>O. montana</u>	<u>Compositae</u>			X	X	X
<u>O. sp.</u>	<u>Penstemon</u>		X			X
<u>O. sp.</u>	<u>Lupinus</u>			X		X
<u>O. sp.</u>	<u>Compositae</u>				X	X
<u>O. sp.</u>	<u>Leguminosae</u>					X
<u>O. sp.</u>	<u>Penstemon</u>	X				
<u>O. sp.</u>	<u>Penstemon</u>	X				X
<u>O. sp.</u>	<u>Compositae</u>	X				X
<u>O. sp.</u>	<u>Leguminosae</u>	X				

TABLE 3 (cont.)

POLLINATOR SPECIES	PLANT(S) VISITED	COMMUNITY TYPE(S) IN WHICH COLLECTED				
		ALPINE	SPRUCE	ASPEN	PESCUE	SAGE
<u>BEES</u>						
<u>Osmia sculleni</u>	<u>Cryptantha</u>					X
<u>O. sp.</u>	<u>Leguminosae</u>		X			
<u>O. subaustralis</u>	<u>Compositae</u>	X			X	
<u>O. sp.</u>	<u>Penstemon</u>	X				
<u>O. sp.</u>	<u>Penstemon</u>	X				X
<u>Panurginus bakeri</u>	<u>Potentilla</u>	X			X	X
<u>P. cressoniellus</u>	<u>Potentilla</u>				X	
<u>P. n. sp.</u>	<u>Potentilla</u>				X	
<u>Pterosarus albitarsis</u>	<u>Compositae</u>				X	
<u>P. n. sp.</u>	<u>Compositae</u>				X	
<u>WASPS</u>						
<u>Pseudomasaris marginalis</u>	<u>Phacelia</u>			X		
<u>P. vespoidea</u>	<u>Penstemon</u>					X
<u>BEETLE</u>						
<u>Coscinoptera vittigera</u>	<u>Potentilla</u>				X	X
<u>BUTTERFLIES</u>						
<u>Boloria helena</u>	<u>Compositae</u>	X				
<u>Nymphalis milberti</u>	<u>Compositae</u>	X			X	
<u>Euphydryas anicia</u>	<u>Compositae</u>	X				
<u>Speyeria hesperis</u>	<u>Compositae</u>		X		X	X
<u>BEEFLIES</u>						
<u>Villa harveyi</u>	<u>Compositae</u>	X			X	X
<u>Anastoechus melanohalteralis</u>	<u>Compositae</u>					X
<u>Conophorus painteri</u>	<u>Compositae</u>					X
<u>Poecilanthrax alpha</u>	<u>Compositae</u>		X		X	X
<u>P. signatipennis</u>	<u>Compositae</u>					X
<u>P. willistoni</u>	<u>Compositae</u>					X
<u>Villa eumenes</u>	<u>Compositae</u>				X	X
<u>SYRPHID</u>						
<u>Vollucella bombylans</u>	<u>Compositae</u>				X	



TABLE 4.

	(BASED ON ABUNDANCE)				(BASED ON BIOMASS)				Plant Biomass Resource Diversity H
	Diversity H	% H Specialists	% H Generalists		Diversity H	% H Specialists	% H Generalists		
SAGE	4.3	8%	70%		2.8	4%	70%		2.3
FESCUE	4.2	2%	76%		2.7	1%	88%		2.3
ALPINE	3.7	0%	78%		2.7	0%	91%		1.5
SPRUCE	3.5	0%	88%		2.3	0%	96%		1.8
ASPEN	3.7	6%	91%		1.7	0%	94%		0.2

TABLE 4. Diversity of Specialist versus Generalist Bees

Diversity is measured by  $H = -\sum(p_i) (\ln p_i)$  ; where  $p_i$  is the proportion  $p$  of the  $i$ th species in the sample. Diversity measured with respect to biomass is less than that measured with respect to individual abundance because the most abundant insects are disproportionately larger than the rest of the fauna.  $\%H$  is the ratio formed by the specialist or generalist  $H$  value (each a subset) divided by the total  $H$  diversity for the entire community. The percent specialist plus the percent generalist does not sum to 100% since there is an entire spectrum of feeding types intermediate between these two extremes.

follow a similar pattern. An average of 82% of the diversity of all pollinators is composed of extremely generalized feeders (Table 4). This proportion increases to over 90% in each of the forest communities and drops to 70% in the sage. "Generalist" is defined in this context as those species which visit more than 7 plant species in only one community. Diversity measured with respect to biomass is less than that measured with respect to individual abundance because the most abundant generalists are disproportionately larger than the rest of the fauna.

Observations in adjacent regions indicate that none of the specialist species cited above consistently use a single plant species, with the exception of an undescribed species of Andrena associated with Erythronium grandiflorum. Many of the resident specialists are restricted in their feeding habits to the tribal level only. The groups most commonly involved in this type of herbivore/plant coevolution are the Leguminosae: Papilionoideae; Compositae: Astereae and the Senecioneae. Potentilla and Penstemon are associated with several specialist taxa and Mertensia, Erythronium, Phacelia, Campanula, and Lupinus are each visited by a specialist solitary bee. With the exception of Erythronium, however, nearly all of the genera pollinated by specialists are heavily visited by generalist foragers as well.

The only plant that we observed to be pollinated exclusively by specialist pollinators is Erythronium grandiflorum, the first flower to bloom each year in the grassland community. (D. Inouye has observed that hummingbirds occasionally frequent it as well in this locality -- pers. comm.) It is visited by an undescribed species of Andrena which is presumably physiologically adapted to the earliest spring in subalpine Colorado. The bee is relatively large, completely black, and very hairy; such adaptations provide maximal solar heating and maximum conservation of heat. Campanula rotundifolia is primarily dependent upon a specialist solitary bee for pollination. Its pendent, bell-shaped flowers apparently interfere with visitation by generalist pollinators which cannot, or do not attempt to, locate the pollen and/or nectar rewards. Dufourea maura, the Campanula specialist, possesses an array of morphological adaptations similar to the Andrena which forages on Erythronium.

Ipomopsis aggregata, Collomia linearis and Androsace septentrionalis are the only other plants which generally are visited by only one species of pollinator. Ipomopsis excludes all pollinators except hummingbirds by means of its extremely long, narrow, tubular corolla. (Visitation by Papilio gothica [Watt, et al., 1974], an endemic swallowtail butterfly, and Hyles lineata [D. Inouye, pers.

comm.], a sphinx moth, have been recorded in the research area, but was not observed by the authors at our particular study plots.) Although they are generalist foragers, the hummingbirds which visit Ipomopsis are nevertheless very efficient pollinators. Through their territorial behavior, the birds themselves regulate the number of competing hummingbirds, assuring a cornucopia of nectar. Pollen remaining in the flowers after the heavy visitation by hummingbirds is harvested by the bee, Lasiglossum trizonatum, even though it cannot penetrate to the base of the corolla to obtain any remaining nectar. This visitation contributes nothing to the pollination of the plant. This pollen-gleaning foraging pattern on post-receptive flowers is similar to that observed on evening primroses in the Sonoran Desert (Linsley et al., 1963). Ipomopsis is also "nectar-robbled" by Bombus occidentalis on occasion; this species does not serve as a pollinator.

Collomia linearis and Androsace septentrionalis are genetically self-compatible and in many regions reproduce by habitual selfing. As the two most common and widely distributed annual plants in an area dominated overwhelmingly by long-lived perennial plants, they allocate little energy to floral production (flowers are 2-4 mm in diameter), while diverting most energy to the production of numerous tiny seeds easily dispersed short distances by wind and water. Both species are very abundant in the disturbed soil of frost heaves and the tumulus of rodent burrows. Bombylius aurifer, a parasite of bee species which nest in disturbed, bare soil, searches for bee nests by hovering at the level of the flowers, 20-40 mm above the ground. As a result, Bombylius frequently encounters both plant species and may visit many flowers in rapid succession, transferring pollen with considerable efficiency.

#### B. Pattern of Resource Allocation by Bumblebees.

Of all the generalist feeding pollinators, none are more abundant or more important to the greatest percentage of plants in the community than the bumblebees. Though they vary markedly in total and relative abundance from year to year, they still are the major pollinators in all communities even when there are relatively few bumblebees as in 1974. The social habits of bumblebees entail a long colony life-cycle and necessarily intense resource utilization; bumblebees must necessarily be opportunistic feeders. Indeed, of all the bumblebees that have been studied (Free and Butler, 1959; R. Thorp, pers. comm.), there is no indication that any American species is genetically specialized upon a given plant species or group (but see Loken, 1961). Any restriction in diet breadth that might occur is a function of local patterns of resource presentation and competition.



Since bumblebees are the most important pollinator group and since they are capable of utilizing nearly any resource present, the key to understanding the pollination dynamics of alpine and subalpine ecosystems revolves around the precise mechanisms which determine bumblebee host choice, population size and distribution.

The resident bumblebee fauna is quite diverse, consisting of at least 11 species. These species divide the available habitats to a considerable degree. Bombus kirbyellus and B. frigidus are usually restricted to alpine tundra; B. frigidus has been found by other workers at lower altitudes in the Gothic vicinity. Bombus mixtus, B. appositus, B. occidentalis, B. rufocinctus, B. nevadensis, and B. californicus are found primarily in the open, subalpine communities. Bombus flavifrons is primarily a forest dwelling and grassland species. Bombus bifarius and B. sylvicola are eurytopic; they are the only other species to be found in abundance within the forests, but never as frequently as B. flavifrons. There are few other studies available in other regions of Colorado to enable us to evaluate the generalizability of these observations. MacIor (1970) reports on the distribution of bumblebee species along the Front Range of the Rocky Mountains near Boulder. He found that B. kirbyellus (= B. balteatus) and B. frigidus were alpine species ranging to over 4,700 m; that B. bifarius and B. sylvicola were distributed throughout all communities between 2,700-4,000 m; and that B. flavifrons and B. mixtus were generally distributed, but most common in the forests and absent in the alpine. Bombus occidentalis occasionally is encountered in alpine regions, spanning the altitudinal range from 1,700-4,700 m.

Habitat division in bumblebees is to a certain extent physiologically based. The two true alpine species are considerably larger and bulkier ( $\bar{x}$  length = 19.8 mm [♀♀], 12.7 mm [♂♂];  $\bar{x}$  body size = 0.99 cm<sup>3</sup> [♀♀], 0.30 cm<sup>3</sup> [♂♂]) than many of those found at lower altitudes ( $\bar{x}$  length = 16.1 mm [♀♀], 11.5 mm [♂♂];  $\bar{x}$  body size = 0.61 cm<sup>3</sup> [♀♀], 0.23 cm<sup>3</sup> [♂♂]). Since the larger body size with its diminished surface/volume ratio is such a clear competitive advantage in harsh environmental situations, it is unclear why the alpine species do not invade lower elevations and outcompete the smaller Bombus in these communities. The reproductives produced later in the year are highly mobile and they do descend to lower altitudes. In 1974 this descent may have been atypical, since the alpine habitats had suffered severe drought stress and the reproductives may have descended in response to a resource gradient. Perhaps the selective factor which does not permit permanent colonization by alpine species at lower altitudes is the apparent tendency of alpine species to produce much smaller colony sizes than the lower altitude

species. If the subalpine species are genetically determined to produce large numbers of small-sized workers in regions under which they can physiologically exist, then they would hold a competitive advantage over the alpine species in subalpine environments. The queen to worker ratio we encountered in the alpine B. frigidus and B. kirbyellus (mean = 1:1.3) is strikingly less than the eurytopic B. occidentalis (1:5.6) or any of the subalpine species (mean = 1:9.6; range 1:6.6 - 1:14.0); we have no direct measurements of the relative colony size.<sup>1</sup>

There is a remarkable degree of diet specialization by Bombus in this region. If, as we have implied in Section I, pollinators are generally so infrequent that competition by most plant species for vectors usually is stronger than competition among bees for limited resources, then optimal foraging theory reviewed by Cody (1974) would predict that during periods of unlimited resource a bee individual may specialize upon the best possible resources while ignoring the majority of blooming plants. The males of most resident species adhere to these predictions closely. They are generally produced late in the summer when the diversity of plant flowers is quite high, yet confine their floral visitation to only the most prolific floral rewards. They forage primarily upon Chamaenerion, Frasera and late summer composites, with B. bifarius, B. flavifrons and B. frigidus confined nearly exclusively to the latter category.

Throughout the growing season, however, an average of only 29% of the flora is heavily dependent upon bumblebees for regular pollination. Instances of individual bumblebees foraging upon nearly every chasmogamous plant species are observed, implying that these bees are sampling the entire community but restricting their prime activity to only those plant species which are providing the most suitable rewards (Figure 1).

The foraging behavior of three Bombus species is notable in this regard. Bombus occidentalis is the only species which "robs" flowers by cutting through the perianth of flowers with nectaries that it is unable to reach with its relatively short mouthparts (Table 5). It does not exhibit any preference for pollen plants, which it exploits in the conventional way, but exhibits a strong nectar preference for Delphinium and Aconitum (also substantiated by D. Inouye, pers. comm.). These flowers not only provide

<sup>1</sup>These ratios are probably highly dependent upon local conditions and should not be taken as characteristic of the species in other regions or even of the same population during years of differing resource availability; rare species were excluded from consideration. These ratios are biased in that many queens probably never found successful colonies and that once a colony is successfully started the queen has a much lower likelihood of being captured on flowers than her workers.

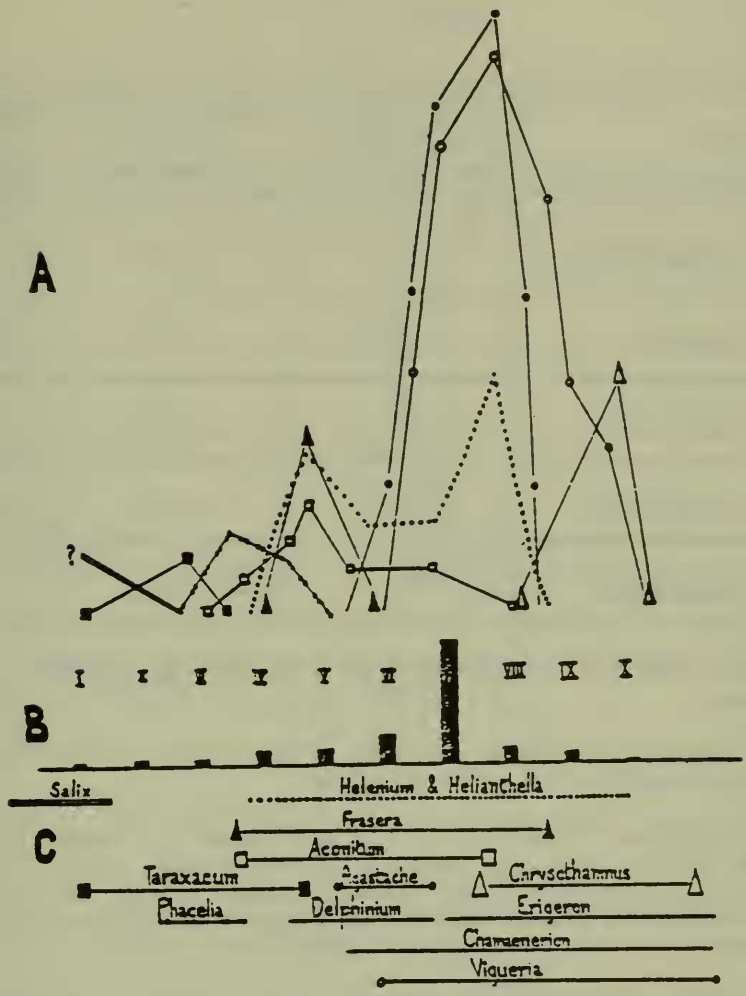


FIGURE 1. Seasonal Resource Utilization by Bumblebees in the Fescue Grassland.

A) Relative abundances of all bumblebee species on the preferred resources from weeks I to X of study. For the sake of clarity, the curves of bees utilizing *Erigeron*, *Delphinium* and *Chamaenerion* are omitted; they peak precisely over the center of the anthesis times.

B) Relative abundance of bumblebee workers and queens on all resources of the fescue grassland during period.

C) Periods of peak anthesis of the most frequently used bumblebee resources; periods of scattered blooming are not included. Note that the bees utilize *Taraxacum*, *Aconitum*, *Helenium*, *Helianthella* and *Fraseria* during only a short portion of their peak blooming season and that *Agastache* and *Phacelia* are the preferred resources even after they have passed their major blooming season.

TABLE 5.

species	total length of head with mouthparts	length/width facial dimensions	length of glossa
<u>B. occidentalis</u>	7.7	1.08	4.2
<u>B. bifarius</u>	5.9	1.13	4.4
<u>B. sylvicola</u>	7.0	1.15	4.4
<u>B. flavifrons</u>	8.9	1.50	5.8
<u>B. appositus</u>	10.3	1.24	6.8

TABLE 5. Facial Morphology of Dominant Bumblebee (Bombus) species.

Measurements represent average values (mm) from five randomly selected workers of each species.

quantitatively some of the largest nectar resources available in the region, but as shown by Watt et al. (1974) produce nectar rich in dimer and trimer sugars which more efficiently fuel bumblebee and hummingbird flight than the usual glucose, fructose and sucrose nectars (Percival, 1961).

Bombus appositus possesses the longest and most slender mouthparts of all the resident bumblebees and therefore is capable of extracting some nectar from spurs without the necessity of robbing the flower (Table 5). This species restricts much of its foraging to Delphinium and Aconitum. Bombus flavifrons, another rather long-tongued species, emphasizes Delphinium and Aconitum in its diet also. Unlike B. occidentalis, both species collect the pollen as well as the nectar of these ranunculaceous plants. MacIor (1970) reports that B. appositus also visits Pedicularis crenulata along the Front Range, another plant which produces voluminous nectar with unusual dissolved sugars (Moldenke, unpub. data).



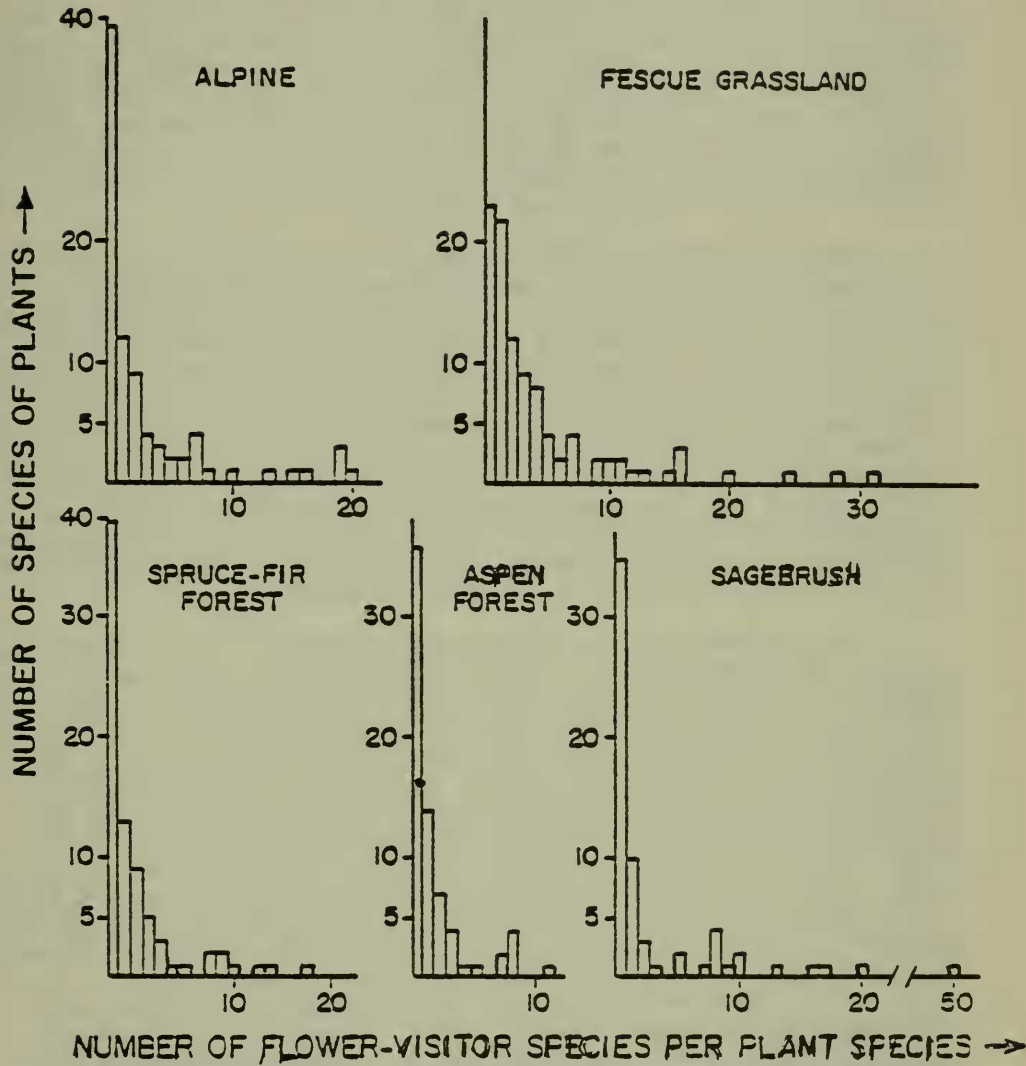


FIGURE 2. Distribution of Total Flower Visitors in Each Community.

Anemophilous plant species are not included. In all communities there are many species visited by 0-2 pollinators and very few species which are visited by large numbers of insect species.

### C. Overlap in Resource Utilization Modes

All communities studied manifest a pattern of food resource division in which many plants are visited by 0-2 pollinator species, much fewer by 3-7 species, and a very few plant species attract large numbers of vector species (Figure 2). This pattern is consistent with observations made in eleven communities in California (Moldenke, 1975). Cornucopia plant species which attract a disproportionate percentage of the pollinator fauna (Mosquin, 1971) are present in all communities examined.

Our operational definition of cornucopia is a plant species which attracts a percentage of the available pollinator species greater than five times the mean number of pollinator species per plant species in the community. This definition is generalizable because it permits comparisons among communities with strikingly different levels of pollinator diversity and is unambiguous. The mean percentage of available pollinator species that the "average" nonwind-pollinated plant species attracts ranges from only 2.2% to 3.3%, while the "average" cornucopia species attracts a disproportionate 12.3% to 20.0% (Table 6). Such cornucopia species are visited by more pollinator species than 92% to 96% of the plant species in each community.

The demarcation for cornucopia species was estimated simply by inspection of the distribution of pollinator species on plant species from our Colorado study (Figure 2). When the same definition of cornucopia species is applied to eight low- and high-altitude California communities, the percentage of cornucopia plant species in each community ranges from 1.0% to 4.6%. The average percentage of the pollinator species attracted to such cornucopia species is also similar to the Colorado results, ranging from 13% to 30%, with an average of 18.8% at high altitudes and a closely approximating 16.0% at sea level. The cornucopia plants from comparable high altitude California study sites are in many cases congeners of those from Colorado communities. Cornucopia species in alpine and subalpine Colorado are Astragalus molybdenus, Aster spp., Chrysopsis villosa, Chrysothamnus spp., Erigeron spp., Geranium richardsonii, Geum rossi, Hymenoxys grandiflora, Ligusticum porteri, Potentilla fruticosa, Potentilla gracilis, Senecio spp. and Taraxacum officinale. With the exception of the first species, all of these plants have a polyphilic floral

TABLE 6. Community Pollination Characteristics and Cornucopia Plants.

Cornucopia species is operationally defined as a plant species which is visited by more than five times the mean percentage of pollinator species per plant species in the community.

TABLE 6.

COMMUNITY TYPE	Number of Pollinator Species	Number of Cornucopia Species	Percentage of Nonwind- Pollinated Plant Spp. Which Are Cornucopia	Mean % of Pollinator Species Visiting Cornucopia Species	Number of Specialist Pollinator Species
FESCUE GRASSLAND	160	4	4.0%	16.6%	34
SAGE	145	3	4.7%	20.0%	32
ALPINE TUNDRA	109	6	7.2%	16.5%	18
SPRUCE-FIR FOREST	77	4	5.1%	16.6%	6
ASPEN FOREST	70	5	7.1%	12.3%	9

morphology which allows exploitation by a wide range of floral herbivores.

Cornucopia species are most numerous in the alpine tundra and aspen forest communities, both in terms of their absolute numbers and in their percentage of the total number of plant species per community (Table 6). However, the alpine tundra has some of the most effective cornucopia plants, based upon the average percentage of total pollinator species attracted to them, while the aspen forest has the least effective. The single most effective cornucopia species in our research sites is found in the sage; Chrysothamnus viscidiflorus is visited by 34% of the resident pollinator species. Not surprisingly, there are few other cornucopia in the sage; the sage community has the fewest cornucopia species. Fescue grassland is the only community having a lower percentage of its plant species which act as cornucopia than the sage. Spruce-fir forest has the same number of cornucopia species as the fescue grassland, but they comprise a larger percentage of the community's total plant species than those of the sage.

Seventy-four percent of all specialist pollinators utilize the cornucopia plant species (Table 3) and hence overlap entirely in their diet breadths with a maximum number of other species. The number of specialist pollinator species increases from 8% to a high of 22% in the most diverse pollinator faunas (Table 6). While this might imply an increase in niche overlap of pollinators in regions of high pollinator diversity, the small relative contribution of specialists to over-all pollinator diversity in all communities (Table 4) makes the true degree of niche overlap difficult to discern in this manner. Niche overlap values calculated directly by the method proposed by Hendrickson and Ehrlich (1971) and adapted by Moldenke (1975) in fact reveal an inverse correlation between total number of pollinator species and degree of niche overlap (Table 7). Despite the distinctly overlapping food utilization strategies of specialists in association with cornucopia plants, their contribution to overlap values calculated on the basis of relative abundance must be minimal. Therefore, decreasing overlap values in pollinator rich communities must be due to a more equitable distribution of generalist feeding species upon available resources.

This inverse correlation cannot be used to determine the nature of niche packing in more diverse communities, since either the narrowing of diet breadths by generalists or simply their diffusion upon more resource states (without a change in the number of resources utilized) could be responsible for decreasing overlap. Changes in niche structuring in species-rich communities are indicated,



however, by the positive correlation between diversity of pollinator biomass and degree of niche overlap (Table 7). This tendency for an increasingly disproportionate biomass concentration upon few resources implies an actual narrowing of diet breadth by those pollinators which comprise the greatest relative amount of biomass in all communities, i.e., Bombus species and hummingbirds. Therefore, it appears that in communities with more pollinator species, the additional species exist by a progressive increase in specialized feeding habits commensurate with a decrease in the tendency of the total fauna to utilize resources in common. This conclusion is supported by the lower number and percentages of cornucopia plant species in communities with the greatest pollinator diversity (Table 6), which must reflect at least indirectly a reduced amount of resource utilization overlap of all pollinators in these communities.

### III. AUTOGAMOUS PLANTS AND VECTOR LIMITATION

Autogamous selfing occurs to some extent in all communities we have studied to date (Moldenke, 1975, 1977, 1979). Generally, selfing is used by annual plants in the understory of a community. Even though some dominant plants may be capable of self-pollination, they seldom have to rely upon it because they are efficiently cross-pollinated. Since the reproductive strategy of selfing is usually confined to annual plants, the occurrence of only nine species of annual plants in all communities studied in Colorado would indicate a weak incidence of selfing in this habitat. All of the resident annual plants are indeed habitual selfers under most conditions. In addition, many of the perennial plant species in the alpine tundra are self-pollinated in the apparent absence of sufficient vectors as reported above. Within the alpine tundra community, eleven (55%) of the twenty most abundant plants are genetically capable of selfing and presumably frequently do so. Higher levels of habitual selfing have been encountered previously only in offshore island and subalpine marsh communities (Moldenke, 1977).

Ten percent of the flora of all the Colorado communities reproduce either by obligate selfing or apomixis. Comparable emphasis on obligate selfing and apomixis is encountered in alpine and subalpine California. The only other systems known to support levels of more than six percent obligate selfing and apomixis are the coastal dunes and bluffs, weedy community and serpentine grasslands (Moldenke, 1977).

Fewer than 2,500 flower-visiting insects were collected in all the research areas during the four person-months of study. While collection techniques are not completely

VECTOR ABUNDANCE			VECTOR BIOMASS		
Total Species	M	M <sub>H</sub> -M	M	M <sub>H</sub> -M	
FESCUE	160	.029	.037	.141	.518
SAGE	145	.026	.531	.153	.448
ALPINE	109	.049	.616	.165	.271
SPRUCE-FIR	77	.071	.622	.208	.433
ASPEN	70	.037	.670	.403	.200

Table 7: Diversity and Niche Overlap of Pollinators

Increasing tendency of the indloes is indicated by the direction of the arrows.

Simpson's "M":

$$M = 1 - \frac{\sum_{i=1}^s \left[ \frac{n_i}{N} \right]^2}{N^2 - N}$$

Hendrickson's "M<sub>H</sub>":

$$M_H = 1 - \frac{\sum_{i=1}^s \left[ \frac{n_i}{N} \right] \left[ \frac{\sum_{j=1}^s (d_{ij})(n_j)}{N^2 - N} \right]}{N^2 - N}$$

where:

M = total number of Individuals

s = number of species

n<sub>i</sub> = number of Individuals in the i<sup>th</sup> species

(d<sub>ij</sub>) =  $\frac{\text{number of food sources utilized by } i \text{ not also by } j}{\text{total number of food sources of } j}$

comparable with the California studies and direct comparison is not possible, Colorado studies yielded at most only 1/10 to 1/25 the number of pollinators that previous studies have documented in low- to middle-altitude regions. Since a large proportion of the pollinators within any community use the same resource plant, communities with more available pollinators may on occasion consequently exhibit higher percentages of the flora relegated to selfing. For example, the sage has nearly the same pollinator abundance as is characteristic of the alpine tundra, but the percentage of the resident plant species that are habitual selfers is half that characteristic of alpine regions.

#### DISCUSSION

Communities in subalpine and alpine Colorado support only one-third to one-half of the total number of species in the more propitious climatic regimes previously studied in California. The mean number of pollinator species per community in these Colorado sites is 113 (Table 1). Studies of three community types (chaparral, oak woodland, grassland) on the Stanford University campus (sea level) in California revealed an average of 377 pollinator species per 0.5 km<sup>2</sup> community sample site (Moldenke, 1975). Another transect including three community types (chaparral, ephemeral community following a chaparral burn, montane oak woodland) in southern California revealed a similarly high level of pollinator diversity with an average of 257 species per community (Moldenke, 1979).

Comparing directly the alpine and subalpine regions of California and Colorado, we expected to find comparable reductions in diversity as a result of the similarly harsh and unpredictable climates at altitudes in excess of 3,300 meters. Alpine tundra in California had 24% fewer pollinator species than Colorado, while subalpine communities in California had twice the number of species found at comparable altitudes in Colorado (California  $\bar{x}$  = 232, Colorado  $\bar{x}$  = 113; comparable areas and analogous community types studied). The relatively greater number of species in alpine Colorado correlates with the larger expanses of true alpine tundra in the Rocky Mountains and may reflect the general species/area relationship (MacArthur and Wilson, 1967) which has never been precisely quantified for any group of pollinating insects. Alpine tundra in the Sierra Nevada of California is restricted to extremely narrow, discontinuous bands of isolated habitats. The numbers of total plant species censused in the alpine communities of both regions are somewhat comparable (California = 78; Colorado = 100), but again reflect the lower species count of California alpine communities.

The total number of pollinator species in subalpine regions of Colorado is only 62% of the number in climatically harsh Colorado Desert of California and is very similar to the very low pollinator diversities of the maritimal bluffs and dunes along the California coast (Moldenke, 1975, 1979). There are no comparable studies for lower altitudes in Colorado, but on the basis of observations made while commuting between our research sites and consultation with Prof. Lanham (Natural History Museum, University of Colorado), we believe that local pollinator diversity increases markedly below 2,750 meters, but never reaches the high levels characteristic of low- or mid-elevation California.

In regards to only bee species, the aforementioned total Stanford University site has 276 bee species (sum of five 0.5 km<sup>2</sup> areas) and the cumulative southern California research sites (sum of four 0.5 km<sup>2</sup> areas, excluding the faunistically unique desert) by 264 total bee species (Moldenke, 1975, 1977, 1979), while only 157 bee species are found within the sum of four 0.5 km<sup>2</sup> sites in subalpine and alpine California. A sum total of 108 different bee species in the comparable five sites in Colorado demonstrates both the tendency for decreased species richness at high altitudes and the decreased richness of the total bee fauna in Colorado relative to California.

All of the results presented confirm the principle that the physiognomy of the community is correlated with, and perhaps exerts a major effect upon, the abundance and diversity of pollinators. Therefore, physiognomically distinct but adjacent community types may support radically different numbers and species richness of vectors. Since the diversity of pollinators is related in part to the breadth of their diet and overlap upon resources utilized in common, the relative emphasis upon different breeding systems within any community is therefore indirectly determined by community physiognomy.

It might be argued that the similarity observed between California and Colorado subalpine pollination systems represents the outcome of parallel evolutionary selective factors acting on separate components of the continuous Arcto-Tertiary Geoflora and Nearctic insect fauna. Though less than 5% of the pollinator species and less than 10% of the plant species is shared at the specific level between the two regions, the majority of the organisms are very closely related (i.e. congeneric) and little more than allopatrically distinct. However, the similarity of trophic relations and diversity patterns between similar community types in the disjunct areas cannot be ascribed to taxonomic similarity alone. The overlap of species within the four high altitude California



communities is much stronger than any overlap between the two mountain ranges, and vice versa. When the same species of plant occurs in more than one community, in no instance is its breeding system identical; even if the same major pollinator occurs in both situations, its abundance and often its fidelity to the plant in question is altered. Self-compatible plant species may rely upon inbreeding more frequently in shaded or climatically more severe environments.

That herbivore dependencies upon the flora assume similar patterns in such widely separated research sites implies that optimal foraging theory (Cody, 1974) applies to assemblages of hundreds of sympatric species as well, so long as the resource bases are comparable. Resource division by bumblebees has been shown to result in similar outcomes of the competitive exclusion principle in Colorado.

The same plant groups in both high altitude Colorado and California have coevolved with specialist pollinators. Seventy-five percent of the plant genera in Table 3 support oligoleges in the California sites as well; only one of the cases of noncorrespondence involves a plant genus not native to the California research sites as well.

Despite the very close over-all similarity demonstrated between these regions, we cannot conclude that the precise pattern of feeding specialization and overlap observed in one season's collecting characterizes these communities on a long term basis. In fact, it is probable that the exact pattern of which species feeds on which plant resources varies greatly, since most of the potential pollen vectors are generalist feeders and the most common species (i.e., Bombus spp.) are liable to very large changes in relative abundance from year to year (D. Inouye, pers. comm.). In addition, there may be large annual fluctuations both quantitative and qualitative in floral resource presentation (e.g., Frasera; Beattie, et al., 1973).

June is typically a period of drought in the study area, but the melting of accumulated snow usually provides a persistent source of water until the onset of thermal storms in July (Langenheim, 1962; D. Inouye, pers. comm.). In the summer of 1974, however, snow melt-water virtually disappeared in the period prior to the first thundershowers; many species of fescue grassland, sage and alpine tundra plants showed signs of drought stress. Veratrum and the late summer composites bloomed exceptionally heavily after the initiation of the rainy season (D. Inouye, pers. comm.). Frasera, which is not controlled by the summer rains (Beattie et al., 1972), also bloomed very heavily in 1974. Another unusual occurrence was that only two individual plants of the extremely abundant Vaccinium species were observed in flower throughout

the entire region. In view of the large variations in the pattern of floral presentation from year to year, it might be expected that the degree of facultative specialization exhibited by potentially generalized feeders would be altered in subsequent years.

Despite potentially broad adaptive responses by certain generalist feeders to changes in resource presentation, there are features of relative species packing in differing community types which remain distinctive. These characteristics involve the relative abundance and diversity of major pollinator groups and the relative emphases upon divergent foraging strategies.

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